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Palaeontology

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4. Palaeontology

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Schweizerische Paläontologische Gesellschaft,
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4.1

Re-evaluation of the fossil cetaceans from Switzerland

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Fossil cetaceans (whales and dolphins) from Switzerland and other paratethyan localities (e.g. Austria, Hungary and Slovakia) are poorly understood, yet their fossil record is relevant to large-scale hypotheses on the evolution of cetaceans. It has been proposed that a marked pulse in cetacean radiation during the Late Miocene was driven by abiotic factors, including the closure of the Tethys (Steeman et al., 2009). To single out the independent roles this and other drivers is necessary to focus on finer-scale studies covering different geographic locations. Regionally, reappraisals have been published for cetacean fauna of the Mediterranean (e.g. Bianucci and Landini, 2002) and the North Sea (e.g. Lambert, 2008). Here, we build on Pilleri's (1986) effort to describe the fossil cetacean fauna of Switzerland, which is now outdated.

The taxonomy of the Swiss cetaceans is particularly challenging: only isolated remains of fossil rostra, mandibles, teeth, earbones, and vertebrae have been found. So far, we have restudied and identified material in four collections, with many smaller collections still to be visited. Our preliminary results indicate an absence of delphinids (*contra* Pilleri, 1986) and a fauna mainly composed of physeteroids (today represented by sperm whales) and a diverse range of platanistoids (today represented by the Ganges river dolphin), including the families Squalodontidae and Platanistidae.

The fossils in the J. Jost and B. Lüdi collections are precisely dated. Most cetaceans are from the Safenwil-Muschelsandstein (Luzern Formation, ca. 19 Ma) and the Staffelbach-Grobsandstein (St. Gallen Formation, ca. 18 Ma). The fossil sharks and rays from the Safenwil-Muschelsandstein indicate a shallow water setting, while the Staffelbach-Grobsandstein fossils indicate deeper water.

The taxonomy of Swiss physeteroideans was reanalyzed by direct comparison of the holotypes at the Royal Belgian Institute of Natural Sciences in Brussels: *Eudelphis mortezelensis, Placoziphius duboisi, Orycterocetus crocodilinus*, and *Physeterula dubusi*). Taxonomic adjustments are a sign of the health of the science of taxonomy (Pyle and Michel, 2008), and this ultimately permeates on all research with taxonomic content, including the widely-used Paleobiology Database.

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4.2

Palaeomeryx (Mammalia, Artiodactyla) and the giraffes, data from the ear region

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Palaeomeryx is an okapi to deer-like animal that was abundant throughout Europe in the Early to early Late Miocene. Very few complete skulls (Duranthon et al., 1995, Rössner, 2010) and no complete or partial skeleton of the European Palaeomerycidae are known. Qiu et al. (1985) described a complete skeleton of a Chinese *Palaeomeryx* but the bad preservation on a slab prevented any in depth-analysis. Its peculiar morphology and the presence of cranial appendages that look like the giraffid ossicones have long been a matter of debate. *Palaeomeryx* and the other representatives of its family (e.g., *Ampelomeryx*, *Germanomeryx*) were supposedly considered sister taxa to Giraffidae (Ginsburg, 1985). A sister group relationship to Cervidae has been proposed for *Palaeomeryx* (Janis & Scott, 1987) and is now mostly accepted.Very few isolated ossicones were found and only the preservation of complete skulls of *Ampelomeryx* from the Early Miocene of Spain and France (Duranthon et al., 1995) revealed how these appendages were positioned on the skull. This lead to propose affinities of the Palaeomerycidae to the North American Dromomerycidae, sometimes included as Dromomerycinae in the Palaeomerycidae family (Prothero, 2007).*Palaeomeryx* and its relatives are thus mostly known through isolated tooth material, or more or less complete jaws. This taxon gave its name to the *Palaeomeryx*-fold, a structure of the lower molars that is common to many primitive members of Ruminantia.

Here we investigate the petrosal bone and the bony labyrinth of *Palaeomeryx* and compare it to both living giraffids: the giraffe (*Giraffa camelopardalis*) and the okapi (*Okapia johnstoni*). Four isolated petrosal bones of *Palaeomeryx kaupi* from the French Early Miocene MN4 locality Artenay, one skull fragment of *Palaeomeryx eminens* from the German Middle Miocene MN7/8 locality Steinheim were CT-scanned and the inner ear was segmented and reconstructed. A juvenile and an adult giraffe petrosal bones together with an adult okapi petrosal bone were CT-scanned and reconstructed too. A work in progress on the bony labyrinth in the deer lineage since the Early Miocene provides the comparative basis for plesiomorphic and derived states in stem Cervidae and Cervidae.

Although the giraffe and the okapi petrosal bones look different, they are close to one another, e.g., they both have a double transpromontorial sulcus on the promontorium, a similar subarcuate fossa or a blunt anterior process of the tegmen tympani. *Palaeomeryx* has a different petrosal bone with a single transpromontorial sulcus, a relatively smaller tegmen tympani or a larger fossa for the tensor tympani muscle, like in the white-tailed deer *Odocoileus*. The bony labyrinth of *Palaeomeryx* is fairly different from that of *Giraffa* or *Okapia*. While both extant genera share a quickly diverging vestibular aqueduct, or a flattened cochlea, *Palaeomeryx* shows a straight vestibular aqueduct, running parallel to the common crus (a very much deer-like condition), a rather massive cochlea mimicking the plesiomorphic condition in the deer lineage, or a lateral canal branching within the posterior ampulla, much like in deer but also reminiscent of the condition seen in the okapi. The giraffe has a different branching pattern, higher than the ampulla and closer to the vestibule.

Our data on the ear region cannot firmly indicate if the hypothesis of affinities of *Palaeomeryx* to deer is more supported than that to giraffes. Data on Miocene giraffes are still lacking and a complete understanding of plesiomorphic characters in the ear region of pecoran ruminants is not yet fully achieved.

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4.3

Ontogenetic variation and heterochronic processes in the cranial evolution of early saurischians

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Heterochrony describes phenotypic changes in evolution due to shifts in the timing or rate of developmental processes in an organism relative to its ancestor. Two primary processes are recognized: paedomorphosis and peramorphosis.

Paedomorphosis occurs when the later ontogenetic stages of an organism retain characteristics from earlier ontogenetic stages of its ancestor, whereas a peramorphic organism is ontogenetically more developed than the later ontogenetic stages of its ancestor (Klingenberg 1998).

Within dinosaurs, non-avian saurischian skulls underwent at least 165 million years of evolution and shapes varied from elongated skulls, such as in the theropod *Coelophysis*, to short and box-shaped skulls, such as in the sauropod *Camarasaurus* (Weishampel *et al*. 2004).

A number of factors have long been considered to drive skull shape, including phylogeny, dietary preferences and functional constraints (e.g. Witzel & Preuschoft 2005, Foth *et al*. 2013). However, heterochrony is increasingly being recognized as a major factor in dinosaur evolution (e.g. Bhullar *et al*. 2012).

In order to quantitatively analyse the impact of heterochrony on saurischian skull shape, we analysed five ontogenetic trajectories (*Massospondylus*, *Coelophysis*, a megalosaurid taxon, *Allosaurus* and *Tarbosaurus*) using 2D geometric morphometrics in a phylogenetic framework consisting of 35 saurischian species. In this framework we evaluated how heterochrony affected skull shape through both ontogenetic and phylogenetic trajectories using principal component analyses and multivariate regressions.

The ontogenetic trajectories sampled show great variation in length and direction, but follow some very general trends (Fig 1a). General peramorphic skulls include more elongate and slender snouts, elongate antorbital fenestrae, oval orbits, dorsoventrally shallower post-rostral regions, and more massive maxillae, jugals, and postorbitals. Paedomorphic skulls show the opposite features.

We found that the hypothetical ancestor of Saurischia led to basal Sauropodomorpha mainly through paedomorphosis in terms of skull shape, while this trend was reversed in basal sauropods due to strong modifications of the snout. In contrast, early theropod evolution was characterized mainly through peramorphosis. Within theropods paedomorphic events occurred two times independently, in basal ceratosaurs and Avetheropoda. The latter event indicates that the paedomorphic trend previously found in advanced coelurosaurs (Bhullar *et al*. 2012) may extend back to the early evolution of Avetheropoda.

Within Avetheropoda, the skull evolution of the large-bodied theropods *Allosaurus* and *Tarbosaurus* was influenced by peramorphosis. Therefore, not only are changes in saurischian skull shape complex due to the large number of factors that affect skull shape, but heterochrony itself is complex, with a number of reversals throughout non-avian saurischian evolution (Fig. 1b).

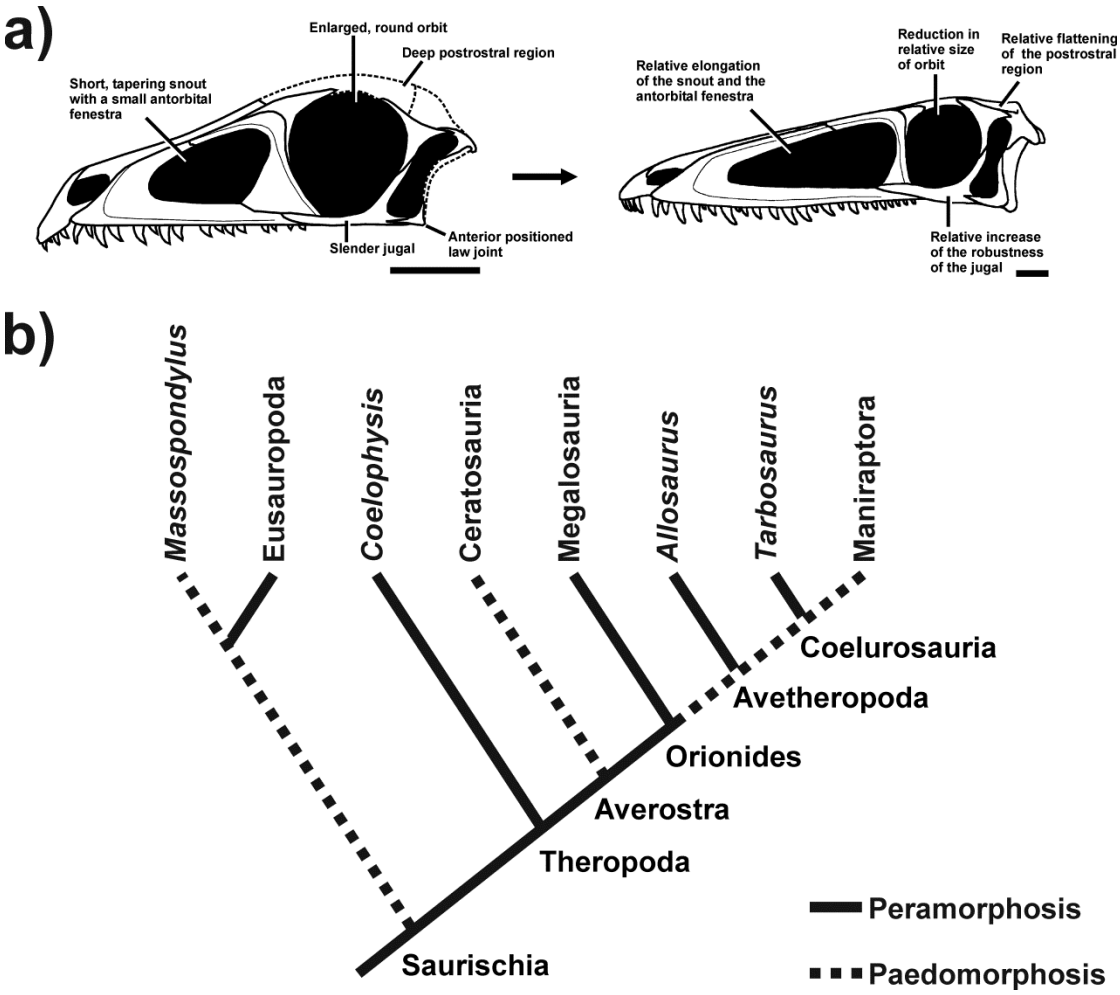

Figure 1 a) Generalized ontogenetic patterns in saurischian skulls exemplified for the basal theropod *Coelophysis* (modified after Foth et al. in review). **b)** Simplified phylogeny of Saurischia showing the main heterochronic trends of the skull. Peramorphosis is shown by solid lines and paedomorphosis by dashed lines.

Bullet list: Dinosauria, Saurischia, Sauropodomorpha, Theropoda, skull shape, ontogeny, heterochrony, evolution, geometric morphometrics

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4.4

Alpha diversity and palaeoecology of a Late Devonian Fossillagerstätte from Morocco and its exceptionally preserved fish fauna

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A Late Devonian Fossillagerstätte with exceptionally preserved fish skeletons, mainly of chondrichthyans, placoderms, and rare sarcopterygians, is known for more than half a century from the eastern Anti-Atlas of Morocco. Although the according localities and parts of their fish contents are long known, some faunal elements have only been found recently. For the first time, we found nearly completely articulated shark specimens including skeletal elements and possibly soft tissue remains as well as abundant phyllocarid crustaceans. In order to reconstruct the preferred habitats and the depositional environment of these fishes, we examine the accompanying fauna for alpha diversity. The excellent exposures of Late Devonian to Early Carboniferous sediments and their faunal associations are rich in invertebrates and allow studying changes in alpha diversity and faunal composition.

We collected several faunas containing invertebrates and vertebrates of early Famennian to early Tournaisian age along two sections in the Maïder region (eastern Anti-Atlas). The specimens of each fauna were determined as far as possible and their frequencies were counted in order to observe changes in diversity. Moreover, the different taxa were grouped to ecological categories of tiering, motility and feeding behavior to describe the ecological diversity within the habitat of the fishes.

Preliminary analyses of the data show a fluctuating species richness through the studied sections. The layers containing the fish remains have a very low diversity in invertebrates with nearly missing benthos and are clearly dominated by phyllocarids. The low number of taxa, in combination with the occurrence of phyllocarids and fishes in iron-rich nodules and the occurrence of small sideritc nodules represent a sea floor sediment deposited under low oxygen conditions, thus yielding a possible explanation for the exceptional preservation. Apparently, nearly perfect environmental conditions prevailed in several phases of the Famennian allowing the preservation of these gnathostome fishes.

4.5

A Revised Global Biogeography of Turtles

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Over the course of the last decades, much effort has gone into unraveling the biogeographic history of turtles, but while much progress has been achieved in resolving post-Jurassic dispersal events, traditional phylogenetic hypotheses have yielded incongruous results in regards to the early history of the group.

Methods.
We re-evaluate the fossil record of turtles in context of recent phylogenetic analyses and fossil finds, including the extensive record of fragmentary but diagnostic remains. However, given that near-coastal and marine turtles readily disperse across aquatic barriers, a broad set of neritic to pelagic groups were disregarded from consideration. Given that significant disagreement still exists among current phylogenetic hypotheses, much effort was placed in tracing unambiguously monophyletic groups through the fossil record. We nevertheless employed molecular backbone constraints, given that the molecular phylogenies are more consistent with the fossil record than current, morphological phylogenies.

Results.
Among derived, aquatic turtles, we recognize four clades that can be traced back to four discrete biogeographic centers: Paracryptodira in North America and Europe, Pan-Cryptodira in Asia, Pan-Pelomedusoides in northern Gondwanan landmasses and Pan-Chelidae in southern Gondwanan landmasses. This pattern is partially mirrored by three clades of primarily terrestrial, basal turtles: Solemydidae in North American and Europe, Sichuanchelyidae in Asia, and Meiolaniformes sensu stricto in southern Gondwanan landmasses. Although the exact interrelationships of these clades remain unclear, most can be traced back to the Middle Jurassic.

Discussion.
The conclusion that the two primary lineages of pleurodires and paracryptodires can be traced back to mutually exclusive land masses is not novel, but the realization that the early history of pan-cryptodires is restricted to Asia has not been realized previously, because traditional phylogenies implied an early, global presence of pan-cryptodires. The timing of the origin of the three primary clades of derived turtles (i.e., Pan-Pleurodira, Pan-Cryptodira, and Paracryptodira) correlates with the opening of the central Atlantic and the formation of the Turgai Strait in the Middle Jurassic, somewhat later than predicted by molecular calibration studies. The primary diversity of extant turtles therefore appears to have been driven by vicariance. A similar hypothesis could also be formulated for the three clades of basal turtles that survive at least into the Late Cretaceous, but given that their combined monophyly remains uncertain, it is unclear if their diversity was also driven by vicariance, or if they emulate a vicariance-like pattern. Although most groups remained within their primary geographic range throughout their evolutionary history, the dominant vicariance signal was thoroughly obfuscated by rich dispersal from littoral to marine turtles and crown cryptodires.

4.6

A Famennian Fossillagerstätte in the eastern Anti-Atlas of Morocco: its fauna and taphonomy

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Nearly 80 years ago, French palaeontologists discovered Devonian fish remains in the Moroccan desert. Mainly placoderm skulls and shoulder girdles, acanthodian fin spines, sarcopterygian remains and locally abundant isolated shark teeth and fin spines have been recorded from the Tafilalt and Maïder regions. Although nearly the entire Devonian succession yields vertebrate remains, greater abundance and sometimes articulated specimens occur mainly in Frasnian and Famennian sediments.

The Famennian Fossillagerstätten of the eastern Anti-Atlas yielded morphologically complete placoderm and chondrichthyan skeletons in recent years. 3D-preserved skulls of chondrichthyans and onychodontid sarcopterygians offer the possibility to unveil aspects of their internal morphology using CT technology. In these cases, the skulls are embedded in the thickest parts of iron rich nodules. The concretions wedge out and the postcranial skeleton is often not contained or incomplete. Since the nodules are embedded in deeply weathered claystones, the postcranial skeletons are usually heavily fragmented and nearly impossible to extract and prepare. Ssometimes parts of the dermal scales and body outline are preserved, documenting the overall morphology of the fishes.

Remarkably, these vertebrate fossils are associated with the oldest documented cases of pseudoplanktonic crinoids, Moroccocrinus and Mrakibocrinus, which lived attached to drift wood. Additionally, a layer with phyllocarid crustaceans, sometimes with appendages, underpins the identification as Konservatlagerstätte, remotely reminiscent of the Jurassic Holzmaden Posidonia Slate or the Devonian Hunsrück Slate. Vertebrates and phyllocarids occur in flat highly ferruginous nodules containing iron oxides and hydroxides. These are most likely products of a deep weathering of pyrite. Fresh samples extracted from below the weathered zone contain pyritic ammonoids, confirming this hypothesis and suggesting sedimentation in oxygen depleted conditions.

4.7

Morphometric analysis of teeth of fossil and recent carcharhinid selachiens

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The morphological variability of dental structures of carcharhinid sharks within and between the different specimens is unsufficiently investigated. Without knowledge of the species specific parameter exact taxonomic classification of fossil sharks based on their teeth is nearly impossible.

A comprehensive analysis of dental structures of recent carcharhinid sharks for species specific attributes was used to transfer the results to their next fossil relatives. Special attention was directed to morphological comparison between fossil teeth from West Atlantic and Central Asian origin.

Against existing methods a morphometric analysis model was developed that avoids manual data collection by reducing the shape data with a matrix of different transcription methods like distance transformation. The new method of automatic algorithmic morphometry (AAM) defined the crucial species specific attribute complexes by analysing more than 3000 single teeth from 120 individuals of 41 species of recent carcharhinids and tranfered the data into a new developed analysis program along with a special database.

The individual study of every single specimen in terms of ontognetic, sexual respectively mono- / dignath heterodonty as well as intra- and interspecific variance in tooth morphology proofed the fact that identifying carcharhinid sharks just by means of tooth morphological attributes is possible and that these attributes are qualified for systematic purposes. The success of the systematic classification is highly depending on the tooth position and the investigated species. The heterodonty influence on the taxonomic significance is occasionally tremendous wich strongly reduces the unambiguity of the classification.

An enormous bandwidth in morphological overlap and interpenetration within the severall species as well as across species and genus leve is existing. Within the comprehensive study using just single teeth of fossil or recent origin it is sometimes impossible to clarify if there is just a innerspecific variance or already a species specific difference.

From the results of the morphometric analysis and the tranfer of the data to the fossil record resulted the necessity to evaluate fossil teeth of carcharhinid sharks not just with the existing descriptive methods of taxonomy but also to use more aspects of functional morphology. Therefore six functional morphologic groups where defined for the first time whereby ecological conclusions are possible.

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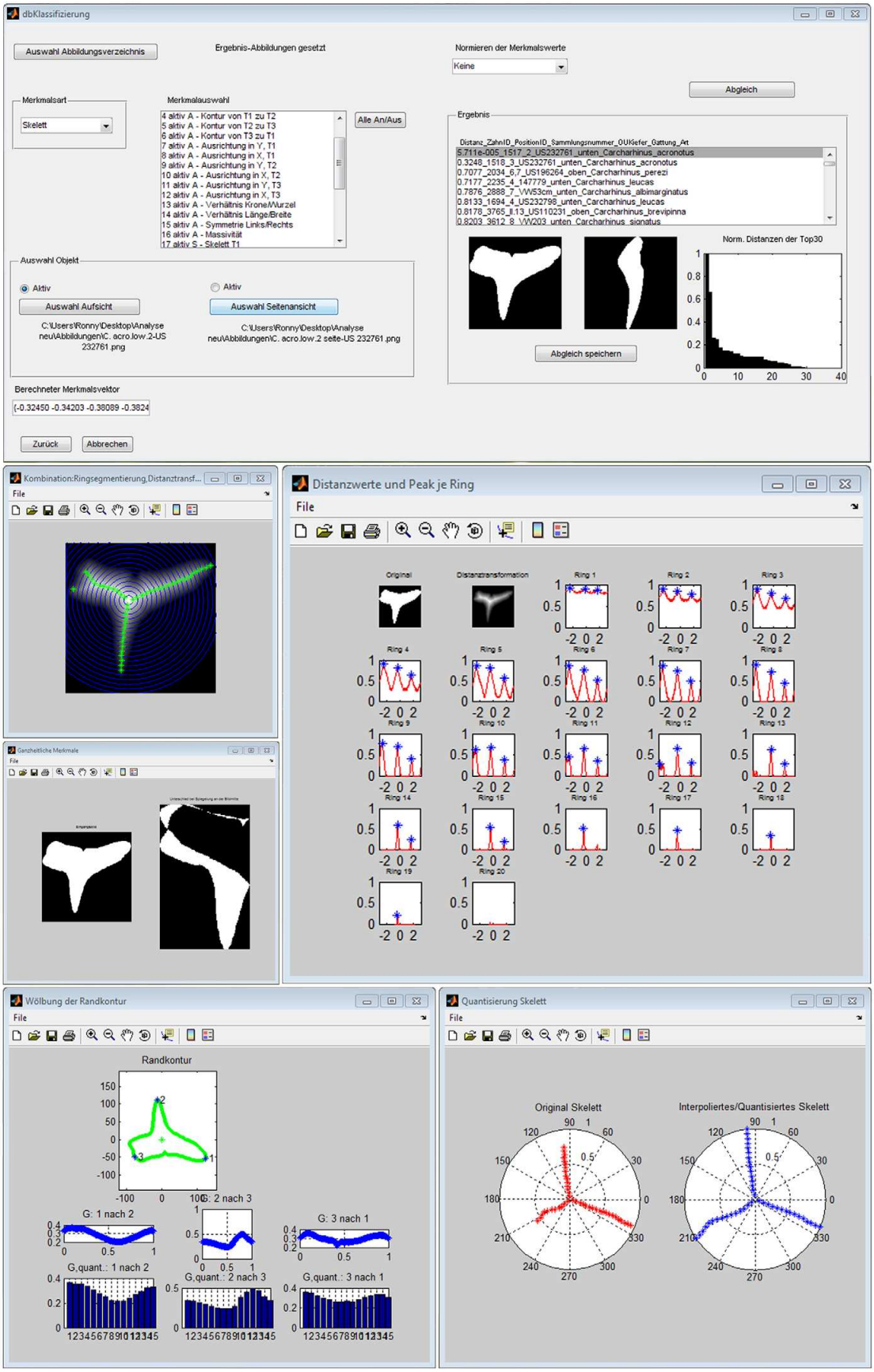

Figure 1. classification mask of the morphometric analysis program (AAM) with the transcription components of the data reduction. Leder 2014

4.8

The diversity of Pleistocene Camelidae in El Kowm, Syria: craniodental remains

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Family Camelidae (Artiodactyla, Mammalia) includes some very important domestic animals from the Old World and South America, such as Bactrian camel, dromedary, llama and alpaca. However, the origins of the family and most of its fossil species were found in North America. The first camels are known from the middle Eocene (Uintan NALMA, ~45 Ma) (Honey et al. 1998), while their maximal diversity was reached in the Miocene, when at least 13 genera and 20 species lived at the same time (Semprebon and Rivals 2010). Camelids colonized Eurasia and South America at the end of the Miocene, and went extinct in North America at the end of the Pleistocene.

The first camelids known in the Old World are recorded in the late Turolian (MN13, Messinian, ~6 Ma) (Van der Made et al. 2002) and are included in *Paracamelus*. Early species were much larger than modern camels; later species survived in the Black Sea region until the early Pleistocene (~2 Ma). This genus is considered paraphyletic (Geraads 2014) and was ancestral to the modern forms. Four fossil species of *Camelus* have been described: *C. grattardi* Geraads 2014 (Ethiopia, 2.2 Ma), *C. sivalensis* Falconer & Cautley 1836 (Indian subcontinent, 2 Ma), *C. thomasi* Pomel 1983 (Algeria and Morocco, middle Pleistocene) and *C. knoblochi* Nehring 1901 (Russia and central Asia, middle-late Pleistocene).

Although the North American fossil record is well studied, the diversity and evolution of camelids in the Old World is poorly known, with few species accurately described and unclear phylogenetic relationships. In particular, there is no founded hypothesis about the ancestry or the domestication of the two recent camel species (*Camelus bactrianus* and *C. dromedarius*).

There are few Old World sites with abundant camel fossils that may help clarify this issue. One of them is the El Kowm Basin, Central Syria. The composed stratigraphic sequence from the several sites in this region spans from the Early Pleistocene (1.8 Ma) to the Late Pleistocene (50 Ka), and is very rich in archaeological and paleontological remains (Le Tensorer et al. 2011). The fauna is dominated by Camelidae, Equidae, Rhinocerotidae and Bovidae (gazelles, larger antelopes and buffaloes) with scarce remains of Carnivora, Suidae, Elephantidae, Struthionidae, Testudinidae. This composition suggests the same arid steppe environment as existing today. The fauna includes the same major taxa throughout the sequence, but the species represented varied over time.

Paleontological studies of the El Kowm collection are underway. Here we present provisional result, with a focus on the cranial and mandibular remains of camelids. In this study we include samples from the three sites of the El Kowm Basin that were excavated by the University of Basel: Nadaouiyeh Aïn Askar, Hummal and Aïn al Fil. Together, they cover most of the temporal sequence known from the region.

The mandibular material can be divided into two well-defined, very different morphological groups. The first is a sample of 9 specimens from the Mousterian cultural levels in Hummal, which are archaeologically firmly dated to the Late Pleistocene (130-50 Ka). The second is a single specimen from the Upper Acheulean levels of Nadaouiyeh Aïn Askar, which are dated to the Middle Pleistocene (520-320 Ka). There is only one fairly complete cranium, also from Nadaouiyeh. Both the cranium and the two forms of mandibula are unlike any known form and likely represent new species. Additional fragmentary material from these and from other layers suggests an even greater morphological diversity.

The cranial and postcranial material studied so far indicates that a minimum of five camel species differing in size and morphology lived in the El Kowm area over the last 1.8 Ma. This number is already greater than the total of fossil *Camelus* species known to date. However, the actual diversity of camelids in El Kowm was likely even higher: there are non-diagnostic specimens that cannot be assigned to the well-known forms, and most of the material is unstudied yet. Therefore, this region provides a unique opportunity to study the evolution of these charismatic animals.

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4.9

Processing and analysis with ‘Cadence Toolset’ of Late Jurassic dinosaur track data systematically acquired during ten years of excavations prior to construction of Highway A16, NW Switzerland

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Excavations along Highway A16 by the Palaeontology A16 from 2002-2011 recorded 59 ichnoassemblages (>17,000 m^2) comprising nearly 14,000 tracks (including 254 sauropod and 409 tridactyl trackways), providing systematic documentation (field measurements, sitemaps, (ortho)photographs, 3D-laser scans), plus the preservation of 700 track-bearing slabs and 200 casts with a total surface of >700-800 m^2.

The track data are currently in the processing (standardisation, cross-checking) and analysis phase (2012-2018), whereas vectorising of sitemaps (global track positions) and assembling of trackway parameter measurements (relative track positions) in a data base are important tasks, constituting the two major, non-relational data sets.

Since 2012 an ichnological data base and software toolset called ‘Cadence’ has been developed and used to extract and integrate information from the sitemaps with the trackway parameter measurements to create an extensive trackway data base for statistical data-mining and analyses. ‘Cadence’ introduces to ichnology the explicit association of uncertainty estimates with all quantitative data, entered through an interactive 3D-graphical interface.

Uncertainty estimation helps control the propagation of error within computations, and permits sophisticated, multivariate statistical analyses between and within individual trackways based on the internal integrity of relative and global measurements. ‘Cadence’ permits exploration of potential relationships with a minimum of a priori conventional assumptions about the trackmakers (such as of hip height, gleno-acetabular distance, gauge, gait), and may provide more defensible conclusions about trackmaker size, identity, locomotion, and even social behaviour and interactions.

This approach builds from a purely geometrical description of the data by avoiding pitfalls such as the subjective interpretation of a smooth ‘trackway path’ and by introducing ‘curvature’, a geometrical curved trackway path that will necessarily be described in terms of uncertainty and with minimal biological interpretation.

The Cadence Toolset is applicable to other data sets in the animal kingdom and collaborations (e.g., of 3D-track morphometric variation, substrate properties and mechanics).

4.10

A new approach to determine the phylogenetic relevance of the bony labyrinth: the case of the Cervid lineage

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In the last decade, studies based on inner ear morphology flourished thanks to easier access to computer tomography. This structure is deeply associated to the locomotor system and proved to be a source of relevant phylogenetic information. Inner ears in Mesozoic mammals, marsupials, xenathrans, elephants, primates, or rodents are currently under study, while that of ruminants, (one of the most diversified group of living large mammals) remains understudied (Costeur 2014). These analyses usually present classical descriptions, but morphometrics and geometric morphometrics have started to be employed. Unfortunately, the use of geometric morphometrics provides a phenotypic tree and these studies often fail to account for instraspecific variability. Moreover, many discrete morphological characters cannot be taken into account in such analyses.

Here we propose to test the phylogenetic relevance of the inner ear morphology based on comparisons of this structure in extinct and extant Cervidae. Stem antlered Cervidae such as *Procervulus* and *Lagomeryx* are known as far back as 18 Ma. The relationships within the living deer are stable and the phylogenetic trees resulting from molecular data (mitochondrial and nuclear) are similar. However, no phylogeny based on morphological characters alone reflects the molecular-based results. Moreover, controversial results on divergence time between the groups have been proposed, mainly because of the lack of consensus on the relationships among the fossil cervids. For example, the emblematic *Megaloceros* is part of the basal radiation of *Cervus* according to molecular data, of the *Dama* radiation in combined analyses (molecular and morphological), or even closely related to the "basal Cervini" *Eucladoceros* when morphological characteristics are taken into account (e.g. Lister *et al*. 2005).

Using a superimposition process ("Landmarks" software), direct comparison between selected inner ears was made. We observed the bony labyrinth of 21 cervid species, including all living tribes and several taxa from key periods: the Early Miocene (origin of stem deer), the Middle Miocene (possible crown deer) and the Plio-Pleistocene (origin of today's disparity). Intraspecific variability was characterized. Between two specimens (*Capreolus capreolus*, extant) and six specimens (*Procervulus praelucidens*, Early Miocene), the differences between juveniles and adults, or intraspecific variability are observed.

Similarly to what is observed among the Tragulidae ruminants (Costeur and Mennecart, in prep), no large intraspecific differences are observed. The size of the semicircular canals and the angle between the canals may vary a little, such as the size of the endolymphatic sac. The total cochlea length can also vary by as most as half a turn. However, these differences are smaller than the interspecific variability. Stem deer can easily be distinguished in having the plesiomorphic characters of a large first cochlear turn, a vestibular aqueduct that is aligned with the common crus. The distinction between the living Capreolinae and Cervinae can be made on the basis of the insertion of the lateral semicircurlar canal into the posterior ampula. Cervinae retain the primitive aspect having a high insertion, while in the Capreolinae, the connexion is lateral. This Capreolinae apomorphic state demonstrates that *Croizetoceros pyreanicus* is the oldest indubitable Capreolinae (6 Ma), even if Late Miocene species have been tentatively attributed to this subfamily (Croitor & Stefaniak 2009). The differences between the various tribes and subtribes can be done based on the shape and position of the endolymphatic sac. Looking at the inner ear morphology, *Megaloceros* clearly differs from *Eucladoceros* in having a triangular endolymphatic sac, starting below the end of the common crus, much like in to *Dama*. On the contrary, *Eucladoceros* possesses a very elongated endolymphatic sac starting above the common crus. This may be the apomorphy of the *Cervus-Rusa* lineage that would include "*Cervus*" *ruscinensis* as the oldest known representative, dating back to 5 Ma. The general morphological similarities between *Megaloceros* and *Eucladoceros* observed in previous phylogenetic analyses are probably linked to symplesiomorphic characteristics and common evolutionary trends in gigantic size and heavy antlers such as proposed by Vislobokova (2013).

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4.11

The Late Triassic bonebed of Niederschönthal (Norian, Knollenmergel, Füllinsdorf BL) – Amanz Gressly's dinosaur locality revisited

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Since its initial discovery in 1856 the locality of the first Swiss dinosaur remains on the riverbank of the Ergolz (Niederschönthal, Füllinsdorf BL) has almost fallen into oblivion (Rütimeyer 1856). Apart from the description of the remains of *Plateosaurus* (Huene 1908 = *Gresslyosaurus*) discovered by the Swiss iconic geologist Amanz Gressly not much attention was given to this locality. In 1901 Karl Strübin excavated at the same locality without much success (Strübin 1901a,b). Later on, Tanner (1978) shortly described the section and the fossil remains that were collected at the locality during construction work. However, up to now neither the associated fossils nor the depositional environment have gained much attention. Similarly, at the famous *Plateosaurus* locality in Frick (AG) the faunal content was studied in some detail, but the environmental setting is just assumed. In 2009 the orginal locality was temporarily exposed again during the renovation of the small bridge over the river Ergolz and the section was revisited by C. Meyer.

Apart from the well known cranial and postcranial remains of *Plateosaurus*, in Niederschönthal the associated fauna and flora is poorly known compared to the coeval deposits of the Frick locality. Re-examination of the specimens collected by Gressly and others stored in the collection of the Natural History Museum Basel revealed the presence of a highly diverse fauna. Phytosaur remains (osteoderms, vertebrae, cranial fragments, long bones, ilia) constitute the dominant elements belonging to *Mystriosuchus* Huene 1911. Large coniform coprolites, some with freshwater clams inside are also frequent. Plant remains as well as rounded pebbles of charcoal have been collected. Teeth of small theropods, a single plastron fragment of a ?terrestrial turtle and fish teeth are also present as well as remains of hybodontid sharks. The overall aspect of the fauna points to a terrestrial habitat having freshwater ponds and rivers. Postcranial material of *Plateosaurus* is also known from a locality further upstream (ARA Liestal; Museum.BL) that still awaits its description.

Whereas Tanner (1978) attributed a Rhaetian age to the bonebed and interpreted it as a lagoonal deposit in a marine environment, we suggest a Norian age and a somewhat different depositional setting. The sedimentary succession indicates an alluvial plain environment. Channels fill deposits with embedded caliche nodules and bones of varying state of preservation point to short-term high energy "pluvial" events that washed away soils and caracasses of terrestrial vertebrates from the catchment area. The top of these channels contain large fragments of wood that appear to be current aligned. The mud deposits most problably resulted from overbank sedimentation or sheetfloods. Intercalated fine sandstones with numerous thin-shelled pelecypods are seen as indication of a playa lake environment.

In contrast, the dinosaur beds of Frick contain many articulated skeletons of *Plateosaurus*. A complete skeleton of a small coelophysoid theropod with a sphenodontid in its stomach still awaits a formal description. Isolated theropod teeth of unknown affinity are frequent and a complete carpace of a turtle *Proganochelys* was found in a nearby locality. Previous studies suggest a miring of the prosauropods (Sander 1992) based on the taphonomy of the articulated skeletons. This might be the most plausible scenario for some beds although up to now sedimentological evidence is missing. However some bones in both localities (Frick, Niederschönthal) show deep cracks indicating intensive wheatering during long time exposure on the sediment surface. The latter is also known from the famous *Plateosaurus* bone beds of Trossingen (Schoch & Seegis 2013).

The disparity in the faunal composition might either reflect a different taphonomic history or distinct habitats. In order to understand the sedimentary environment as well as the Late Triassic continental ecosystems of northern Switzerland a detailed sedimentological analysis of the dinosaur beds of Frick is in dire need.

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Fig.1 Stratigraphy of Late Triassic sequence of the Ela Park

Figure 2. 3D contour model of a prosauropod manuspes couple (Uglix Plattenkalk Member, Hauptdolomit Group; Val Gravaratschas, Ela Park)

4.12

The Norian and Rhaetian dinosaur tracks of eastern Switzerland in the light of sequence stratigraphy

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Prosauropod and theropod footprints from the middle and upper part of the Hauptdolomit Group (HDG; Mid to Late Norian) from the Upper Austroalpine Ela Nappe in the Parc Ela nature park (Canton Graubünden; southeastern Switzerland) and the Swiss National Park (Engadin Dolomites) provide important information on the paleobiogeographic distribution of the early dinosaurs (Meyer et al. 2010). Up to now, seven levels with dinosaur tracks have been detected in a stratigraphic range spanning the Norian to Late Rhaetian (Fig 1; Meyer et al. 2013). The large theropod tracks from Parc Ela attributed to the ichnotaxon *Eubrontes* (UPM:Uglix Plattenkalk Member of the HDG Group) and those from the Swiss National Park (Diavel Formation) together with the record from the coeval Dolomia Principale of the Tre Cime di Lavaredo (Dolomites, Italy) are the oldest unequivocal evidence of very large theropod dinosaurs. Furthermore trampled surfaces in the upper part of the HDG (Fig.1, 1; Ela Park; Late Alaunian to Early Sevatian) at three different locations indicate the presence of large dinosaurs. At the boundary between the HDG and the Kössen Formation (Aelplihorn Member) a trackway with deep quadradactyl pes prints as well as tridactyl manus prints can be attributed to a facultative bipedal prosauropod (Fig.1, 3; Fig. 2) In the youngest part of the Kössen Formation (Fig 1, 7; Silvaplana Member) sauropod tracks are also present.

The UPM contains at least 3 different levels with tracks (Fig. 1,2-4) the lowermost is a laterally persistent surface that is heavily trampled, these are probably associated with a 4th order sequence boundary. The exact sequence stratigraphic position of the trackbearing levels in the Swiss National Park remains to be determined. The levels in the Diavel Formation are most likely time equivalent with the trampled levels in the middle part of the HDG of the Ela Park. It seems quite possible that the highest levels in the Murtèr Formation and Murteret Dolomite are coeval with those in the UPM. The uppermost track level in the UPM corresponds to the No2 third-order sequence boundary (Gianola & Jacquin, 1998; McCann 2008; Alaunian/Sevatian boundary). This stratigraphic unit is time equivalent with the Knollenmergel of the Keuper that has yielded numerous skeletons of the prosauropod *Plateosaurus* . The sauropod tracks in the Silvaplana Member appear to be situated close to the Rh 2 third-order sequence boundary at the end of a shallowing upward cycle.

The track levels that have been detected in the Dolomites seem to be slightly older than previously sugested by Belvedere et al. (2014). According to our own field observations, the tracks that have been found in the Tre Cime di Lavaredo (Capella Alpini, Cima Piccola, Cima Ovest) and the Averau area are most likely situated at the No1 third-order sequence boundary (Lacian/Alaunian boundary) and therefore older than those from the Swiss sites.

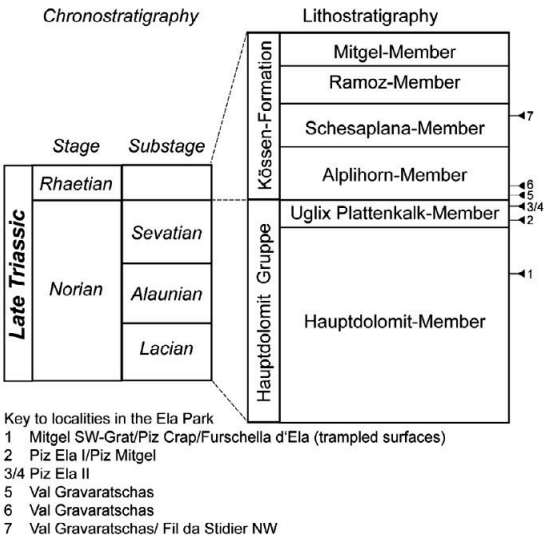

Fig.1 Stratigraphy of Late Triassic sequence of the Ela Park

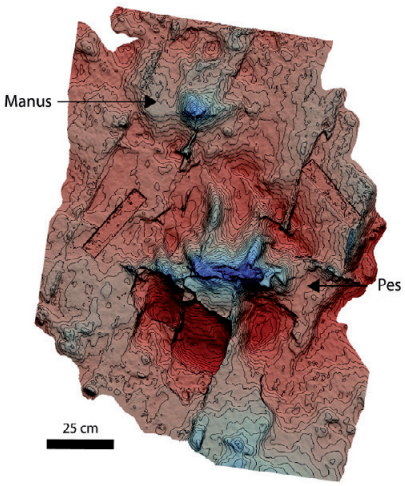

Figure 2. 3D contour model of a prosauropod manuspes couple (Uglix Plattenkalk Member, Hauptdolomit Group; Val Gravaratschas, Ela Park)

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4.13

Evolution and paleobiogeography of reef biota in the Panthalassa domain during the Late Triassic: insights from reef limestone of the Sambosan Accretionary Complex, Japan

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Paleoecology and paleobiogeography of Triassic reef biota are mainly based on the investigation of Tethyan and East Panthalassa reef localities. Conversely, western Panthalassa reef biota were poorly documented until recently. Therefore, reef limestone occurrences from the western Panthalassa domain are pivotal to understand the global Triassic reef evolution. In this contribution, we investigate Upper Triassic reef limestone from the Sambosan Accretionary Complex (Japan), aiming at improving our knowledge of the Upper Triassic reef ecosystem in the huge Panthalassa domain.

The Upper Triassic carbonates from the Sambosan Accretionary Complex record the evolution of diversified shallow water environments from the initiation of the carbonate platform during the Ladinian?-Carnian to its demise in the Rhaetian. Accordingly, the Sambosan limestone yield valuable insights regarding the reef recovery and development that took place during the Middle and Late Triassic. These profound environmental changes and biotic turn over are well-known in the Tethys but poorly documented in the Panthalassa.

Our results provide additional constrains for understanding the evolution and the biogeographic distribution of Upper Triassic reef biota.Quantitative microfacies analysis, combined with an integrated biostratigraphy (i.e., reef biota associations together with conodonts and foraminifer biostratigraphic markers), allow us to well characterize both Ladinian?-Carnian and Norian-Rheatian reef bioconstructions in the Sambosan limestone. To quantitatively compare the Sambosan reef biota with their counterparts, we compiled the occurrences of 186 genera of calcareous sponges, microproblematica and foraminifers from 18 reef areas located in the Tethys and Panthalassa oceans. Multivariate statistics (cluster analyses and ANOSIM tests), based on this taxonomically homogenized dataset, strengthen the Tethyan affinity of the reef biota from the Sambosan Accretionary Complex.

This original study refines the biostratigraphic framework of the shallow water carbonates of the Sambosan Accretionary Complex, considered here as representative of West Panthalassa atoll-type environments. These findings highlight the long geological history of carbonate build-ups in the Panthalassa during the Late Triassic and emphasize the biogeographic connections with the Tethyan domain.

4.14

Catalogues of the palaeontological heritage from the A16 – Transjurane highway (Canton of Jura): example of the Mesozoic marine crocodilians

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After twelve years of intensive fieldwork and now sixteen years of scientific research, the Paléontologie A16 moves into its last three years of activity. Until 2018, and additionally to more than 60 scientific publications, nearly 150 conference presentations and 34 scientific collaborations with students on their way to access different academic degrees, the five remaining research groups will publish their scientific final reports.

One step towards the presentation of the large amount of data and the most important scientific results is the publication of an extensive documentation of the fossil collection, through a series of sixteen catalogues called "Catalogues du patrimoine paléontologique jurassien - A16". With this series of catalogues, the paleontological heritage of the Canton of Jura is made more attractive, for both scientists as well as for a more general public. This can contribute to future investigations such as comparisons with other collections, of contemporary age and from different European localities. Also, all catalogues show a methodological approach that could be applied to valorize other fossil collections.

Here, we introduce this series with a catalogue dealing with the thalattosuchians (the Mesozoic marine crocodilians), from the Kimmeridgian of the region of Porrentruy (Schaefer 2012a, b; Schaefer & Billon-Bruyat 2014). This catalogue shows the most representative specimens of the collection, in order to indicate both the taxonomic diversity and the kind of preserved material. The standardized sheets are composed of scientific (systematics, anatomy, stratigraphy, locality) and technical (related illustrations, analyses, bibliography) information, and specimens' illustrations (photographs, drawings). Two families, four genera and five species are represented (the teleosaurids *Steneosaurus jugleri*, *S.* cf. *bouchardi*, *Machimosaurus hugii*, and the metriorhynchids *Metriorhynchus* sp., *Dakosaurus maximus*), by means of 36 specimens (including skeletons, isolated cranial and post-cranial elements). In conclusion, this catalogue gives a good and quick scientific overview of this crocodilian collection; it will be a helpful tool for future research, conservation, visits and exhibitions.

We gratefully acknowledge all implied experts, such as excavation teams, fossil preparators, illustrators, editors and scientists, which have been involved in the compilation of the document. Our special thanks also go to the Federal Roads Office (FEDRO) and the Canton of Jura (RCJU) for financing this work.

CPPJ Catalogues du patrimoine paléontologique jurassien fiche **TCH006-1439**

Teleosauridae, *Steneosaurus* cf. *bouchardi*

TCH006-1439

Détermination

Famille : Teleosauridae
Genre : *Steneosaurus*
Espèce : cf. *bouchardi*

Anatomie : mandibule
Particularités : –
Détermination (nom / date) : JPBB, KS / 2012

Stratigraphie

Couche : 4500
Lithostratigraphie : Marnes à *virgula* inférieures
Formation : Reuchenette

Biostratigraphie : Eudoxus
Chronostratigraphie : Kimméridgien supérieur

Site

Nom : Courtedoux-Tchâfoué (CTD-TCH)
Unité : 56
Alignement (°N) : –

Coordonnées CH : 250 421 / 568 731
Altitude absolue : 504,87 m

Figures

Photos de studio
TCH006-1439_man_dor_E025_3703.jpg*
TCH006-1439_man_gch_E025_3718.jpg*
TCH006-1439_man_ven_E025_3699.jpg*

Photos de terrain
TCH006-1439_ens_3522.jpg*
TCH006-1439_ens_9591.jpg*
TCH006-1439_ens_9952.jpg*
TCH006-1439_ens_20070914007-36.jpg*

Dessins scientifiques
TCH006-1439_man_dor_E025_val.tif*
TCH006-1439_man_dor_E033_val.pdf
TCH006-1439_man_dor_E033_val.tif*

Relevés de terrain
TCH006-r117 (1:10)
TCH006r.118 (1:1)

Analyses

Géochimie ($\delta^{18}O$ phosphates)

Bibliographie A16

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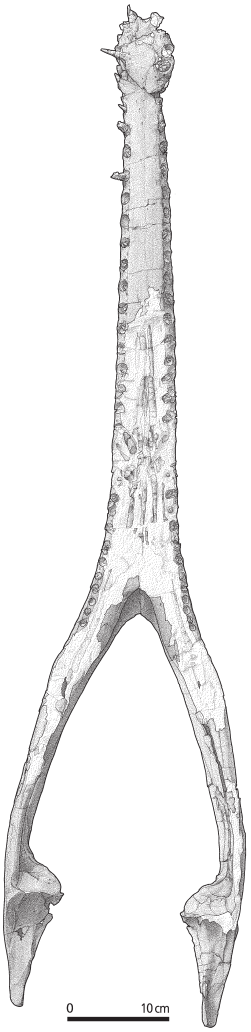

Excerpt from the catalogue: example of the mandible of Steneosaurus cf. bourchardi TCH006-1439 (Late Kimmeridgian, Courtedoux–Tchâfouè). On the left side: scientific and technical sheet. On the right side: scientific illustration of the specimen in dorsal view.

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4.15

Intraspecific variation of volumetric growth trajectories in nautilids and ammonites

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Ammonoids and nautilids are well-known, externally shelled cephalopods. While ammonoids went extinct at the end of the Cretaceous, nautilids survived. Because of their morphological similarity of the external shell, lots of palaeontologists have invesitigated Recent *Nautilus* as an actualistic example to better understand the obscure ammonoid palaeobiology. Despite all the research efforts to explore *Nautilus* ecology and anatomy, phragmocone (buoyancy apparatus) geometry and volume have not been sufficiently studied. However, ammonoids and nautilids are phyllogenetically not the closest regardless of their similar external shells. Ammonoid phragmocones record both growth and palaeoecology. *Nautilus* phragmocones can be an important reference to palaeoecology of fossil nautillids since they have maintained nearly the same shell over a long perioid of time. Comparison of phragmocones of ammonoids and nautilids can provide important clues on differences in palaeoecology, which would have resulted in ammononid extinction and nautilid survival at the end of the Cretaceous.

Only quite recently, empirical volume models of ammonoids have been reconstructed to caluculate buoyancy (Lemanis et al., 2015; Naglik et al., 2015; Tajika et al., 2015). However, all these studies addressed only one specimen per species. These results may thus be biased due to intraspecific variation. Individuals may or may not represent be representative for the taxon. Here we present intraspecific variation of phragmocone chamber volumes in living *Nautilus pompilius* from the Phillipines and of the Jurassic ammonite *Normannites* from Switzerland.

The reconstruction of the ammonite specimens was carried out using grinding tomography. The specimens were ground off and exposed surfaces were scanned in alternation with an increment of 0.06 mm, generating 422 images. Every 4th image was retraced in Adobe® Illustrator (Adobe Systems). Then the retraced image stacks were imported to VGstudiomax®2.1 (Volume Graphics) in which 3D models were constructed. By contrast, 30 *Nautilus* specimens (12 males, 9 females, 9 indeterminable) were reconstructed using Computed tomography. 30 specimens were scanned with a resolution in the range of 0.311 and 0.440 mm. Subsequently segmentation was conducted in Avizo®8.1 (FEI Visualization Sciences Group) and volumes of each chamber were extracted and measured in Meshlab (ISTL–CNR research center) and Matlab 8.5 (Math Works), respectively. The reconstructed two ammonites and a *Nautilus* are shown in Figure 1.

The volumetric growth trajectories of *Normannites* show a very similar trend during early to middle ontogeny.A considerable divergence occured in late ontogeny, most-likely resulting in different buoyancy regulations. In the last several chambers, both specimens desplay a strong fluctuation of volumes. Growth trajectories from *Nautilus* showed a quite high variability, still following logistic curves. In *Nautilus*, chamber volumes were also reduced in latest ontogeny (only in the last chamber). Statistical tests suggest that the shells of the two sexes of *Nautilus* differ only slightly and that there is a strong overlap in morphology between the two sexes. Nevertheless, overall intraspecific variation of all specimens exceeds that of one sex only. Covariation between chamber widths and volumes in *Normannites* and *Nautilus* were assessed. The results suggest that *Normannites* are more flexible in shell construction. *Nautilus* apears to stick to a certain morphology, changing the shape much less than the Jurassic ammonite throughout ontogeny.

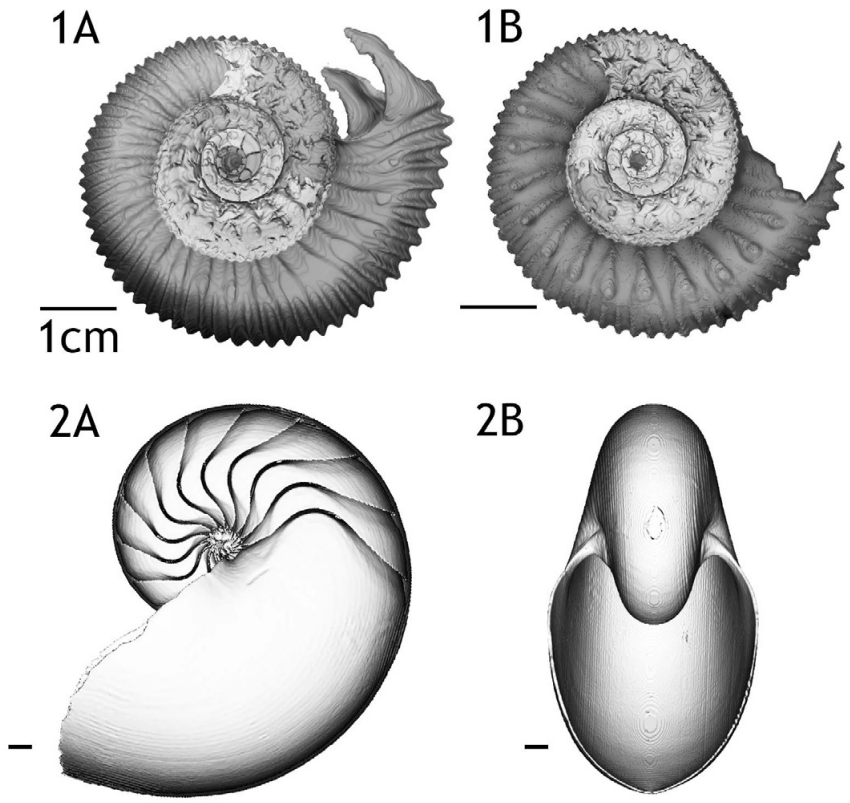

Figure 1. Reconstructed ammonites, *Normannites* and living *Nautilus*. (1A) *Normannites* Specimen 1; (1B) *Normannites* specimen 2; (1C) *Nautilus pompilius*.

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P 4.1

The Fossil Echinoids of the St. Ursanne Formation in the Swiss Jura Mountains

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Since the beginning of the Triassic, echinoids play a prominent role in marine benthic communities (Kroh & Smith, 2010). Although echinoids reached their greatest level of diversity in shallow marine areas (Durham et al., 1966), they also populated the full spectrum of other marine habitats throughout their history, ranging from the poles to the equator and from the intertidal zone to the deep-sea. The echinoid skeleton is composed of a large number of individual elements with complex microarchitecture and therefore provides a rich basis for morphological studies. Given that the skeleton of echinoids is shaped by the environment (Sumrall & Brochu, 2008) and that they are common occurrences in the fossil record, echinoids can be considered to be facies fossils (Kroh & Smith, 2010) and the group therefore features prominently in evolutionary and paleobiological studies.

As part of my master's thesis, I am measuring nine lithostratigraphic profiles from the St. Ursanne Formation in the Swiss Jura Mountains and then correlating the carbonate microfacies of these localities with the fossil echinoids they contain. The latter step requires identifying more than 300 echinoid specimens to species level that were collected over the course of the last 200 years at these localities.

There are no previous studies for the St. Ursanne Formation that examined a possible correlation of echinoid taxa and their respective facies. This work is therefore expected to provide new insights into the sedimentology, lithostratigraphy and paleobiology of this formation.

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P 4.2

Study of the microfauna from the Falun (Langhian, France): preliminary data on the Ostracoda

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The « Falun » formation is a shelly sand, mainly Langhian in age (Middle Miocene). These deposits extend from the French Atlantic coastline, between Brittany and Vendée Regions to westwards to Orléans (Figure 1). It forms the ancient Ligerian Gulf along the current Loire river valley. Since the 18th century, the richness in fossils (e.g. the giant shark *Megaselachus megalodon*) permitted a systematic study of the area. A large diversity of marine invertebrates was described (e.g. more than 600 species of Mollusca). Between 1959 and 2000 more than 35 contributions on mammals were published by Léonard Ginsburg. However, until now, data on microfossils remains scarce. An overview of the regional ostracod fauna reported 53 species (Charrier & Carbonnel 1980), but those were not documented in detail. Benthic Foraminifera have been described for the area of Thenay (Margerel 2009).

Since 2007, the national inventory of geological heritage ("Inventaire National du Patrimoine Géologique") permits an overview of all the Falun localities (predominantly quarries). Prof. J.-J. Macaire and C. le Doussal (local advisor for Indre-et-Loire and Loire-et-Cher) and local authorities provided access to protected geological sites (regional natural geological reserve of Pontlevoy, geological reserve and protected area of Falun d'Amberre) and technical support. Falun deposits from Morvilliers (Chapelle-Saint-Martin-en-Plaine) are for the first time investigated since 50 years thanks to a backhoe. This area represents the most oriental extension of the formation (even if new marine vertebrate fossils are currently under study from the Ouzouer-le-Marché collections). Sediments from Villbarou, picked in a cellar, are also under study. The construction of a new road in falun deposits provided rich vertebrate remains at the industrial zone of Contres (Loir-et-Cher).

A comparison of the fossil record from 15 different localities and 20 different facies is in progress in the oriental part of the "Falun Sea". Initially a study on the ostracod assemblages will be carried out. A preliminary appraisal of several samples allowed the identification of at least 50 species, at least one possibly new. The presence of the genera *Aurila*, *Costa*, *Cytherelloidea*, *Cytheretta*, *Loxoconcha*, *Olimfalunia*, *Cytheridea* (amongst others) indicate shallow marine to nearshore environments, comparable to those reported from the Serravalian of the Aquitaine Basin (e.g. Ducasse & Cahuzac 1997). Even though the variability of the assemblages between the individual localities is rather low (except the species richness), we can observe large differences in the preservation and abundance of the material (from well preserved to eroded, perforated specimens), indicating differences in the environment and position of the Langhian coastline.

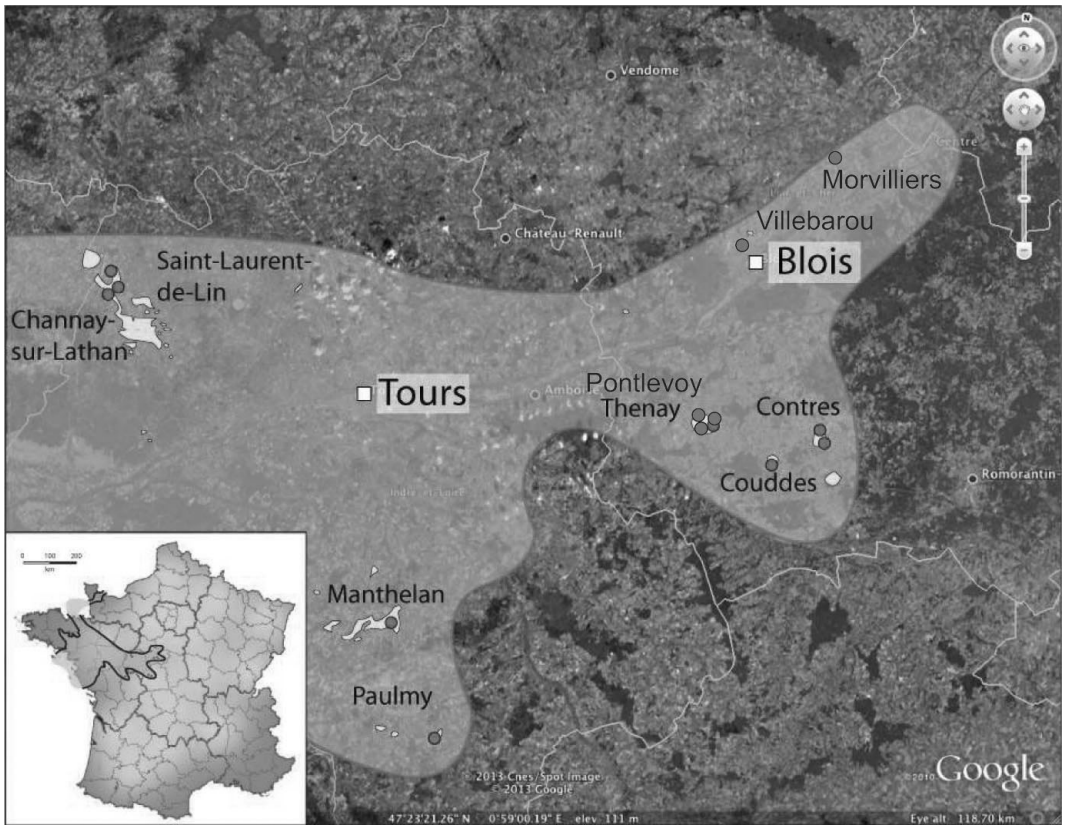

Figure 1. Map of the studied Falun localities (dark dots). The transparent white area represents the maximum extension of the Falun Sea surface. The Falun deposits currently known are indicated in light grey.

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P 4.3

The morphology of the petrosal bone of cats (Felidae) and its phylogeny and paleoecological implications

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The inner ear of mammals consists of the cochlea and the vestibular system, which are housed within the petrosal bone, that is often well preserved in the fossil record because of its compactness (Loïc 2014; Luo et al. 2010). Given that the petrosal surrounds the inner ear tightly, it forms a natural mold, which can be used to reconstruct this soft tissue structure in fossil taxa. However, traditional techniques demanded serially sectioning skulls to investigate the inner ear, thereby fully destroying the specimen.

X-ray computed tomography (CT) allows scanning the inside of a skull without damaging the specimen. This technique has therefore become prevalent in recent years, because it enables reconstructing the internal and external morphology of fossil and recent skulls (Luo and Ketten 1991). The petrosal has hereby revealed itself to be a structure of notable interest, as it preserves many morphological features of paleoecological and/or phylogenetic interest (Spaulding et al. 2009; Ciffli 1982). Although much research had been dedicated to the cranial anatomy of cats (Felidae), only little is known about the morphology of their petrosals.

For my research, I am scanning and digitally reconstructing the petrosals of a broad sample of recent and fossil cats to explore its significance to the paleoecology and systematics of the group.

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